Effects of neighboring woody plants on target trees with emphasis on effects of understorey shrubs on overstorey physiology in forest communities: a mini-review

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Abstract: Plant-plant interaction plays a key role in regulating the composition and structure of communities and ecosystems. Studies of plant-plant interactions in forest ecosystems have mainly concentrated on growth effects of neighboring plants on target trees. Physiological effects of neighboring plants on target trees, in particular understorey effects on physiology of overstorey trees, have received less attention. It is still unclear what is the physiological mechanisms underlying positive growth effects of understorey removal, although understorey removal has been applied to improve the wood production for hundreds of years worldwide. Only 17.5% of published works dealt with understorey-overstorey interactions and only a few of those researched the understorey effects on the physiology of overstorey trees. Case studies indicated that overstorey *Abies faxoniana* trees grown with different understorey shrubs showed significantly different levels of tissue nitrogen and mobile carbohydrates. Removal experiment showed that nitrogen and mobile carbohydrates concentrations in *Cunninghamia lanceolata* trees grown in the absence of understorey shrubs differed significantly (pure stand > mixture) with those in trees grown in the presence of understorey shrubs, in particular during the dry season. This review highlighted that the neighboring woody plants affect C- and N-physiology in overstorey trees. These effects may be mainly resulted from underground competition for soil water rather than for other resources as the effects were more pronounced during the dry season. The present review suggests that positive effects of neighboring removal (e.g., understorey removal, thinning) on overstorey trees can be expected more rapidly and strongly in stressful area (e.g., low rainfall, nutrient-poor site) than in areas with optimal growth conditions. Hence, ecophysiology-based management strategies for dealing with neighboring plants in forest ecosystems should take into account: 1) site conditions, 2) timing, duration and frequency of management practices, and 3) species-specific properties and other aspects such as biodiversity conservation and soil erosion.

Abbreviation: NSC–Non-Structural Carbohydrate.

Introduction

A fundamental question of how plant species stably co-exist in a community is still waiting for conclusive answers in plant community ecology (Silvertown 2004). Coexisting plants interact in many different ways, and plant-plant interaction plays a key role in regulating and determining the composition, functioning and productivity of plant communities and ecosystems (Brooker 2006).

Plants coexist in nature. The co-existing plants in a community may have allelopathic phenomena, and compete for light, nutrients, space, pollinators, and water, but at the same time protect one another from the impacts of herbivores, potential competitors or extremes of climate, and provide additional resources through canopy leaching, microbial en-

hancement, mycorrhizal networks and hydraulic lift (Barot 2004, Balandier et al. 2006, Dudareva et al. 2006, Brooker et al. 2008, van der Heijden and Horton 2009). These interactions will further influence the individual physiological activity determining the growth performance at individual and community level.

Plant-plant interaction occurs in either monoculture (intraspecific) or mixed culture (interspecific and intraspecific). The co-existing individuals of the same species (monoculture) have the same or similar architecture and resource requirement (Keddy 1989, Grace and Tilman 1990). Stable co-existence of different species (mixture) may require them to occupy different niches (Gause 1934, Wilson 1990, Silvertown 2004), in order to acquire resources from external pools (Kuppers 1985, Tremmel and Bazzaz 1995, Grams et al.

2002, Kozovits et al. 2005). These resources are invested to determine the size, morphology, and physiological activity of a plant, which further influences a plant's physiological ability to explore the environment for resource availability (Kuppers 1984, Umeki 1995, Suzuki 2002), and determines the process of resource acquisition (Curran et al. 1999).

Plant size and architecture determine the positioning of leaves and fine roots (Kozovits et al. 2005) and biomass partitioning, which may change in response to neighboring plants of the same or other species (Weiner and Fishman 1994, Tremmel and Bazzaz 1995, Aerts 1999, Aphalo et al. 1999). Natural forests, old growth stands, and unmanaged forest plantations are normally multilayer structures with tall- and medium-size trees, shrubs, climbing vines, and ground vegetation. In such forest ecosystems, the coexistence of overstorey and understorey vegetation is sustained (Kume et al. 2003) under overstorey-understorey interactions.

Although understorey vegetation competes sustained with the coexisting overstorey for space and resource, understorey effects on overstorey trees, especially on the overstorey physiology, have received less attention, because understorey, due to the smaller plant size, is not able to shade the coexisting overstorey's green shoots. In particular, no work studied differences in mobile carbohydrates (soluble sugars and starch) in trees growing in the absence and presence of understorey vegetation, although mobile carbohydrates concentrations and the pool size in trees reflect the balance between carbon gain (photosynthesis) and carbon loss (growth and maintenance respiration) and have been widely recognized as a tree's capital for growth (e.g., Li et al. 2002, Körner 2003). Hence, the present paper, unlike other systematic review papers published (Rothe and Binkley 2001, Binkley et al. 2003, Forrester et al. 2006b, Kelty 2006), will focus on the effects of neighboring woody plants on physiology with emphasis on mobile carbohydrates in desired trees. The aim of the present paper is to explore whether removal of neighboring woody plants in particular understorey shrubs can positively influence the overstorey physiology resulting in enhanced availability of nitrogen and mobile carbohydrates in overstorey tissues. In addition, the present paper will contribute to a better understanding of the functional mechanisms of the effects of neighbor removal which has been applied in forest plantations to improve wood productivity for hundreds of years worldwide.

A statistic overview of plant-plant interaction studies in forest ecosystems

Studies related to plant-plant interactions in forest ecosystems have traditionally concentrated on effects of associated plants/trees on growth (height, diameter, and biomass growth, and stand development and productivity) (46.1%, Fig. 1), followed by tissue nutrients (17.0%, Fig. 1; mainly macronutrients), belowground system including soil nutrients and soil water availability, and microclimate (11.2%, Fig. 1), gas exchange and water use efficiency (8.2%, Fig. 1)

Distribution of published research papers (%)

Figure 1. Distribution of published research papers dealing with plant-plant interaction in forest ecosystems (evaluation of 330 publications found in ISI Web of Science by the end of 2010, using combinations of key words of 1) 'forest*' or 'tree*' and 'competition' and 'facilitation', 2) 'forest*', 'weed control' and 'effect*', and 3) 'overstor*', 'understor*' and 'interaction*'). A research paper that dealt with 2 main subject categories was duplicated even triplicately recorded. This survey did not include research related to allelopathic phenomena, biodiversity and conservation, and mycorrhizal issues. Review papers, PhD and MSc theses were disregarded. Research related to overstorey-understorey interactions has not been further distinguished into other subject categories such as growth and physiology.

of the desired trees. On the other hand, the overstorey-understorey interactions, especially the possible effects of understorey plants on the growth and physiology of the overstorey trees, have received less attention. For example, research related to overstorey-understorey interactions had only a total fraction of 17.5% consisting of overstorey effects on understorey plants (11.1%) and understorey effects on overstorey trees (6.4%) (Fig. 1), and the majority of those 6.4% papers concentrated on weed control for juvenile trees in reforestation or agroforestry systems.

Effects of neighboring woody plants on growth of desired trees

Nearly 50% of the published works dealt with the growth effects of plant-plant interactions in forest ecosystems (Fig. 1), part of which focused on stand-level productivity in terms of total stand biomass, and the another part on individual-tree growth rate in terms of merchantable timber. Recently, many studies concentrated on the facilitative effects of nitrogen-fixing trees/shrubs (e.g., *Acacia* spp., *Alnus* spp., *Casuarina equisetifolia*, *Ceanothus* spp., *Leucaena leucocephala*, *Robinia pseudoacacia*, etc.) on non-nitrogen-fixing target trees (Parrotta 1999, Bauhus et al. 2004, Nichols et al. 2006, Oakley et al. 2006). Many studies examined the growth performance of trees grown in mixtures with a nitrogen-fixing species compared to monoculture, i.e., the inter-specific vs. intra-specific effects on height growth (Groninger et al. 1997, Linden and Agestam 2003, Boyden et al. 2005), pro-

ductivity (Binkley et al. 1992, Parrotta 1999, Bristow et al. 2006, Erskine et al. 2006, Forrester et al. 2006b), C-allocation (Shainsky et al. 1992, Kaye et al. 2000, Forrester et al. 2006a), and stand development (Groninger et al. 1996b, DeBell et al. 1997, Binkley et al. 2003, Kelty 2006). These investigations demonstrated that mixed plantations can achieve greater productivity than monocultures (DeBell et al. 1985, Binkley et al. 1992, DeBell et al. 1997, Parrotta 1999, Forrester et al. 2006b, Kelty 2006, Richards et al. 2010, Richards and Schmidt 2010), and such positive growth effects have been explained as results of enhanced soil nutrients availability and cycling caused by the presence of the nitrogen-fixing species (Carlyle and Malcolm 1986a, b, Parrotta 1999, Rothe and Binkley 2001).

It is widely accepted that N can be transferred from the N-fixing species to the companion species (Kelty 2006). The N transfer mechanism is explained that the soil N availability increased since the soil N pool increased via decomposition of dead leaves and roots with high N contents of those N-fixing plants. An increase in leaf/needle N contents led to increases in photosynthetic rate (Martindale and Leegood 1997, Davey et al. 1999, Kitajima and Hogan 2003, Diaz-Espejo et al. 2007), resulting in higher growth rate and productivity. On the other hand, a mixed stand may use the space and resources more effectively than a pure stand. For instance, in crop science it has been well-documented that the intercropping system greatly contributed to crop production by its effective utilization of resources, as compared to the monoculture cropping system (Cakmak et al. 2007).

Similarly, thinning has generally been recognized to reduce competition and to increase N availability and, further, enhance radial growth of remained trees (Youngberg 1975, Hocker 1982, Harrington and Reukema 1983, Simard et al. 2004). For example, individual stem diameter growth in *Pinus taeda* was found to be 51% higher in thinned stand compared to unthinned stands (Ginn et al. 1991). For Scots pine (*Pinus sylvestris*) at dry sites, quadratic mean diameter increments increased with thinning intensity and the response of diameter growth to thinning was greater in young trees (less than 50 years) and in medium sized trees compared to older ones (Makinen and Isomaki 2004). Both ponderosa pine (*Pinus ponderosa*) in southeastern USA and Norway spruce (*Picea abies*) in Belgium showed a long-term positive effect of decadal thinning on growth over up to 50 years (McDowell et al. 2003, Misson et al. 2003). Such positive and long-term lasting effects of thinning on the remained trees were mainly explained as results of reduced competition and increased resource availability (Youngberg 1975, Hocker 1982, Harrington and Reukema 1983, Simard et al. 2004). But the physiological mechanisms underlying those positive growth effects have been poorly understood so far (Makinen and Isomaki 2004).

Overstorey effects on understorey woody plants

About 11% of the published works dealt with overstorey effects on understorey vegetation such as nurse effects and

overstorey competition (Fig. 1). Facilitation (e.g., nurse effect) and competition effects of overstorey on the germination and recruitment, and seedling establishment of other woody species under a canopy have been extensively reported (Oren et al. 1987, Fulbright et al. 1997, Takahashi 1997, Lloret et al. 2005, O'Brien et al. 2007, Munguia-Rosas and Sosa 2008). Canopy cover is one of the most important factors affecting understorey species diversity and composition in forest stands (Sagar et al. 2008). Overstorey removal led to changes in understorey composition and increase in species diversity (Ram et al. 2004, Elliott and Knoepp 2005). Understorey vegetation was found to change considerably and dynamically with overstorey structure and composition related to canopy cover (Hart and Chen 2006). After canopy closure, understorey composition shifted to the dominance of shade tolerant species with a decline in number, cover, and abundance of vascular plant species but an increase in bryophytes. Consequently, herbaceous production decreased in a linear or nonlinear manner as overstorey timber volume or canopy cover increased (Joyce and Baker 1987). Vascular plant cover was highest under deciduous stands and decreased with increasing conifer content (Legare et al. 2002), indicating that overstorey composition associated with canopy coverage significantly affects the understorey vegetation communities. These studies indicated that the effects of overstorey trees on the understorey vegetation seem to depend on (1) the sunlight reaching the forest floor and (2) on the shade-tolerance of the understorey species (O'Brien et al. 2007, Parker and Dey 2008).

The presence of overstorey canopy can lead to significant reduction in the understorey growth and productivity (Hagan et al. 2009, Manceur et al. 2009, Perry et al. 2009). For example, Hagan et al. (2009) reported that *Callicarpa americana*, *Morella cerifera*, and *Ilex glabra* grown separately alone under a canopy (canopy coverage ~35%) of 15-year-old longleaf pine (*Pinus palustris*) stand, had a biomass reduction of -75.5, -50.6, and -68.7%, respectively, compared to their monoculture (i.e., without an overstorey canopy).

Net photosynthesis and leaf conductance to water vapor of red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) seedlings significantly increased with decreased canopy density of overstorey (Parker and Dey 2008), indicating marked overstorey effects on understorey ecophysiology (Granhus and Braekke 2001). However, the presence of an overstorey canopy of *Prosopis glandulosa* var. *glandulosa* had no effects on the growth and physiology of the understorey shrubs of *Zanthoxylum fagara* and *Berberis trifoliolata* (Barnes and Archer 1999). Perry et al. (2009) found that the physiological responses of understorey to overstorey depended on the species of the overstorey trees (i.e., *Pinus sylvestris* vs. *Fraxinus pennsylvancia* in that study), or varied with understorey species itself (i.e., *Andropogon gerardii*, *Bromus inermis*, *Lotus corniculatus*). Similar results were also reported by Manceur et al. (2009). McKenzie et al. (2000) stated that the relationships between understorey development and overstorey conditions represented both direct resource limitations and time-dependent responses. Hence,

we may conclude that the understorey responses to overstorey are results from overstorey-induced changes in understorey environment such as light availability, substrate, temperature, soil nutrients, and pH.

Effects of neighboring woody plants on tree nutrients

Seventeen percent (17.0%) of the published works related to plant-plant interactions in forest ecosystems investigated nutrients status in tissues of trees grown in mixtures compared to monoculture (Fig. 1). The published data documented either an increase (Carlyle and Malcolm 1986a, Brozek 1990), a decrease (Kozovits et al. 2005), or no change (Groninger et al. 1997, Thelin et al. 2002) in leaf nutrients concentrations in trees grown in pure stands compared to mixtures with other woody plants (Parrotta 1999, Specht and Turner 2006).

Specht and Turner (2006) found that foliar N concentrations of trees (12 species) varied significantly with the co-existing woody species in mixed forest plantations in New South Wales, Australia. Increased tissue N contents were typically found in trees grown in mixtures with N-fixers compared to monoculture, showing a nursing effect of N-fixers on N content in the co-existing trees. For example, leaf N concentrations increased in *Eucalyptus globulus* grown with *Acacia mearnsii* in plantations (Bauhus et al. 2004, Forrester et al. 2005) and in *E. delegatensis* grown with *Acacia dealbata* in a natural forest (Kuppers 1996). Binkley et al. (1984) and Brozek (1990) showed that Douglas-fir (*Pseudotsuga menziesii*) grown in mixtures with alder (*Alnus* sp.) had higher foliar N concentrations than those grown in the absence of alder. Foliar N concentrations of *P. menziesii* increased from 9.3 mg g⁻¹ in monoculture to 14.1 mg g⁻¹ in mixture with *Alnus rubra* (Binkley 1983).

On the other hand, Groninger et al. (1997) found that pine (*Pinus taeda*) foliar N did not vary with stand types (monoculture vs. mixture with *Robinia pseudoacacia*). Thelin et al. (2002) reported that there was no difference in N concentration in current-year needles of *Picea abies* grown in pure stand and mixtures with either beech, birch, or oak, respectively. Kozovits et al. (2005) found that beech grown in mixture with spruce had a significantly lower tissue N content, but spruce trees showed significant enhancement in its tissue N content in the mixed culture, compared to monoculture.

Similarly to those contradictory findings mentioned above, thinning effects on nutrients of remained trees have also been found to be positive, negative, or no effects. Hokka et al. (1996) reported that thinning increased foliar concentrations of N, P, and K in *Pinus sylvestris* trees, and concluded that thinning improved the foliar nutrient status by reducing the competition for nutrients. Velazquezmartinez et al. (1992) found that thinning improved N, K, and Mg concentrations in young trees of Douglas-fir (see also Medhurst and Beadle 2005). On the other hand, Jonard et al. (2006) found that N, P, and K concentrations in current-year needles of *Picea abies* trees were decreased by thinning ($p \leq 0.05$),

while Ca, Mg, and Na concentrations were not affected. They concluded that thinning negatively affected N, P, and K nutrition by removing the nutrients contained in the thinned trees (Jonard et al. 2006).

A recent review paper also revealed that tissue nutrients (N, P) level in trees grown in mixture compared to monoculture varied from case to case (Richards et al. 2010). Hence, we may conclude that the nutrient levels in target trees reflect trees' ability of resource acquisition and resource-use efficiency which depend on the physiology and morphology of the target species itself and the interactions of the species assemblage within a community (see Nambiar and Sands, 1993, Binkley et al. 2004).

Effects of neighboring woody plants on photosynthesis and water use efficiency in overstorey trees

Only 8.2% of the published works related to plant-plant interactions in forest ecosystems investigated biochemical and physiological aspects of carbon metabolism in trees grown in mixtures compared to monoculture (Fig. 1). Richards et al. (2010) pointed out that "there are few examples where rates of photosynthesis have been compared for a given species in monoculture and mixture" (pp. 1200).

The mean light-saturated net photosynthesis rates of *E. globulus* were found to be significantly higher in monoculture (14.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ on a leaf area basis, or 0.053 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ on a foliage mass basis) than in 1:1 mixture with *A. mearnsii* (11.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, or 0.040 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) (Bauhus et al. 2004). In a greenhouse experiment with Loblolly pine (*Pinus taeda*) and Red maple (*Acer rubrum*) seedlings, Groninger et al. (1996b) reported that pure pine had lower photosynthesis rate than mixed pine under either ambient CO₂ or elevated CO₂ (c. 798 ppm) conditions, whereas pure maple had higher gas exchange rate under ambient CO₂ but lower rate under elevated CO₂ compared to mixed maple. Kozovits et al. (2005) found that the sun leaves of beech had similar net CO₂ uptake rate in mono- and mixed cultures with spruce. But under elevated CO₂ (c. 670 ppm), the net CO₂ uptake rates of beech in mixed culture tended to be lower compared to those in monoculture (Kozovits et al. 2005).

Binkley et al. (2004) found that the light-saturated rate of photosynthesis in *Eucalyptus saligna* increased linearly with increasing N concentrations in leaves (see also Kume et al. 2003). Experimental studies also revealed that leaf photosynthetic rates of various plants/trees are positively correlated with leaf N content (Martindale and Leegood 1997, Davey et al. 1999, Kitajima and Hogan 2003, Diaz-Espejo et al. 2007). If an individual has competitive advantage over others for N, water, and other resource, it must be able to (1) acquire a greater proportion of the soil resource, (2) use resource more efficiently for producing biomass, and (3) allocate assimilate in ways that will maximize capacity for growth (Nambiar and Sands 1993).

Hence, it is possible that multispecies mixtures had higher water-use efficiency compared to monocultures, because different plant species can use soil water from different depths of the soil profile due to having contrasting water uptake strategies (Vandermeer 1989, Jose et al. 2006). Forrester et al. (2010) found that for every m^3 of water transpired by *Eucalyptus* trees in mixtures produced more wood and aboveground biomass than those in monocultures in Australia. Again, Forrester et al. (2010) found that annual transpiration was 419, 358 and 217 mm in the 1:1 mixture of *E. globulus* and *A. mearnsii* and in monoculture of *E. globulus* and *A. mearnsii*, respectively. However, at individual tree level, we found that very little is known about water-use efficiency of trees in mixtures compared to monocultures (see also Richards et al. 2010).

Several studies have investigated the short-term effects of thinning on physiology of remained trees. A decrease in stem density was associated with an increase in photosynthesis rate in *Pseudesotoma menziesii* and in *Pinus ponderosa* (Sala et al. 2005). An increase in photosynthesis rate could be partially associated with a decrease in light competition, in particular at the lower crown level (Ginn et al. 1991, Groninger et al. 1996a). In old ponderosa pine stands, thinned stands showed increases in stomatal conductance and carbon isotope discrimination in the wood up to 15 years following the treatment (Groninger et al. 1996c, Jonard et al. 2006). An increase in carbon isotopes discrimination reflected a decrease in water use-efficiency likely due to an increase in soil water availability in thinned stands (Bréda et al. 1995).

Effects of understorey shrubs on overstorey carbon- and water physiology

Only 6.4% of the published works dealt with understorey effects on overstorey trees in forest ecosystems (Fig. 1). Plants that occupy the overstorey layer have a clear advantage in the competition for light. When the overstorey plants develop a dense canopy and shade the understorey plants completely, overstorey plants will be successful in suppressing understorey plants by means of a monopoly of light resources. But a large water supply is also needed to keep dense canopy of overstorey. Spatial and temporal segregation of roots and shoots by neighbouring plants may be an effective strategy for reducing competition for space and resource (Balandier et al. 2006). For instance, shallow-rooted herbaceous species utilize water and other resource in top-soil and deep-rooted woody plants acquire separate resource from deeper soil horizons (Nambiar and Sands 1993, Casper and Jackson 1997, Balandier et al. 2006). However, even with a vertical stratification of root systems, the overstorey trees that have roots in the deep soil layer can also suffer from water deficit caused by dense understorey vegetation colonizing the upper horizon leading to an almost complete withdrawal of soil water in the upper soil layer and to a gradual drying of the deeper soil layers (Balandier et al. 2006). Hence, the understorey may be most likely to affect the overstorey through below-ground competition for soil resources

(Montgomery et al. 2010). For instance, many weed control/removal experiments carried out in tree plantations and agroforestry systems showed that dense understorey weeds led to increased water stress in crop trees (Carter et al. 1984, Elliott and White 1987, Petersen et al. 1988, Nambiar and Sands 1993). Needle water potential of juvenile *Pinus radiata* plants decreased when weeds were present (Sands and Nambiar 1984, Watt et al. 2003), and a negative linear relationship between percentage cover of weeds and *P. radiata* needle water potential has also been reported (Nambiar and Zed 1980).

Miller et al. (1998) carried out an experiment in low rainfall area in New Zealand, and reported that trees (*Pinus radiata*, ~3.4 m in height) grown with an understorey of cocksfoot (*Dactylis glomerata*) had lower xylem sap flux and total canopy conductance than trees grown with an understorey of ryegrass (*Lolium perenne*), indicating that different understorey species imposed different degrees of competition for water on the overstorey trees. Both competition for natural resources between the overstorey trees and the understorey vegetation, and the effects of understorey vegetation on modifying the micro-environmental conditions, may affect the physiology of the overstorey trees, leading to changes in growth rate (see also Fig. 3). For example, Watt et al. (2003) reported that, after 2-years of weed treatment, young *P. radiata* trees grown in the absence of weeds had an aboveground biomass 25-fold greater than that of trees grown in the presence of weeds. To understand the effects of understorey shrubs on overstorey trees, Kume et al. (2003) reported that *Pinus densiflora* trees grown in the presence of understorey shrubs (*Eurya japonica*, *Ilex pedunculosa*, *Symplocos lucida*, *Rhododendron reticulatum*) had smaller maximum net photosynthesis and stomatal conductance but greater needle $\delta^{13}\text{C}$ values compared to trees grown in the absence of the understorey shrubs (removed). They also found that needle nitrogen contents and photosynthetic nitrogen use efficiency in trees grown in the presence of understorey shrubs were lower than in the absence of understorey vegetation (Kume et al. 2003, see also Binkley et al. 2004). Similar photosynthetic responses of *Pinus banksiana* trees to grasses (*Poa pratensis*, *Festuca* spp.) (Mohammed et al. 1998) and *E. globulus* trees to *A. mearnsii* (Bauhus et al. 2004) have been reported. Their results consistently indicated that understorey vegetation negatively affected the physiological activities in overstorey trees, although the understorey species varied among the 3 case studies from grasses (Mohammed et al. 1998) to shrubs (Kume et al. 2003, Bauhus et al. 2004).

Photosynthesis is only one aspect, but what is more important is the carbon balance between carbon gain (photosynthesis) and loss (respiration) within a tree (Körner 2003, Li et al. 2008b). This balance (= carbon gain – carbon loss) is commonly described using the concentration or pool size of mobile carbohydrates (Li et al. 2001, Hoch et al. 2002, Li et al. 2002, Hoch et al. 2003, Körner 2003, Li et al. 2008a, Li et al. 2008b), since mobile carbohydrates represent a tree's capital for growth (Hoch et al. 2002, Li et al. 2002, Körner

2003). Shainsky and Rose (1995) reported that concentrations of starch and TNC (total non-structural carbohydrates) in needles of Douglas-fir (*P. menziesii*) trees decreased significantly in mixture with alder (*Alnus rubra*), but needle sugars did not differ between trees grown in monoculture and mixture.

Li et al. (Li, Pan, Du et al., unpublished data) found that levels of N, non-structural carbohydrate (NSC) and its components (soluble sugars, starch) in overstorey *Abies faxoni-ana* trees varied significantly with the co-existing mid-storey shrubs (Table 1), indicating that (1) co-existing understorey shrubs altered the N and C metabolism in the overstorey trees, and (2) different understorey species with different physioecological properties affected the overstorey physiology differently. To test those findings (Table 1) gained using natural experiments, Du et al. (unpublished) studied the status of N and NSC in China fir (*Cunninghamia lanceolata*) trees grown in the presence and absence of mid-storey shrubs using mid-storey removal experiments. Their results indicated that the presence of mid-storey shrubs resulted in lower levels of mobile carbohydrates in tissues of overstorey trees compared to the absence of mid-storey plants (Table 2, Fig. 2). These studies highlighted the roles of understorey vegetation in determining the carbon and nitrogen physiology of overstorey trees (Tables 1 and 2, Fig. 2). Moreover, Du et al. also found that the understorey effects on N and NSC in overstorey trees differed between the dry season and rainy season (Fig. 2). This may imply that the understorey effects on overstorey trees may be mainly resulted from understorey competition for soil water rather than for other resources in the study area. Hence, positive or negative physiological effects of understorey management on overstorey trees may be dependent on understorey-specific properties (e.g., N-fixers or non N-fixers) (Table 1; see also Forrester et al. 2007 vs. Kume et al. 2003), timing and duration of understorey man-

agement (Adams et al. 2003, Balandier et al. 2006), and also on site conditions (e.g., dry site vs. wet site; Fig. 2).

Effects of understorey shrubs on soil temperature and soil water contents

The understorey effects on overstorey trees, as described above, seemed to result from belowground competition rather than from aboveground interaction. About 11% of the published papers studied the understorey effects on soil temperature, water contents, nutrients, microorganisms, etc. (Fig. 1). It is well-documented that dense understorey vegetation can significantly decrease the soil temperature, net N mineralization, net nitrification rates, and soil water availability (Matsushima and Chang 2006, 2007, Devine and Harrington 2008, Wang et al. 2011, Yildiz et al. 2011, Zhao et al. 2011). Understorey removal can lead to significant increase in soil N (Tripathi et al. 2005, Matsushima and Chang 2006, Tripathi et al. 2006, Matsushima and Chang 2007) and soil water availability (Takahashi et al. 2003, Matsushima and Chang 2007), and consequently, resulting in increased growth rate of the overstorey trees (Oren et al. 1987, Takahashi et al. 2003). For example, we removed the understorey shrubs (~55% coverage) in three forest plantations (*Cryptomeria japonica*, *Taiwania flousiana*, *Metasequoia glyptostroboides*) in southwestern China in April 2008, and measured the soil temperature and soil water contents during the growing season from May to October 2008. Our data (Du et al., unpublished) indicated that the mean growing season soil temperature (-10 cm) and soil water contents were 0.64–1.24 °C and 8.3–9.9% higher in understorey-removed sites than in forest plantations with intact understorey, respectively. Increased soil temperature did not result in decreased soil water contents, indicating that the understorey-transpirational water loss exceeded the faster evaporation caused by

Figure 2. Concentration (% d.m. $\pm$ 1 SD, $n=3$) of total nitrogen, non-structural carbohydrate (NSC) and its components (soluble sugars, starch) in previous-year needles (≥ 1 -yr-old) of *Cunninghamia lanceolata* trees grown in the absence (pure *C. lanceolata*) and presence of mid-stories at 1600 ± 100 m a.s.l. on a gentle SE-facing slope, Chongzhou, SW China (Du, Li, Pan, unpublished data). Needle samples were taken during the dry (May 5–7) and rainy season (September 22–26) in 2009. Statistical differences were tested using one-way ANOVAs, and followed, if significant, by Tukey's HSD test. Different letters indicate significant differences at $p < .05$. n.s., $p > .05$. See note for Table 2.

	Total N				Soluble sugars				Starch				Non-structural carbohydrates			
	2-yr-old needles	Fine roots	Sapwood		2-yr-old needles	Fine roots	Sapwood		2-yr-old needles	Fine roots	Sapwood		2-yr-old needles	Fine roots	Sapwood	
<i>Abies-Rh.</i>	1.33±0.03	0.84±0.07 ^a	0.11±0.01 ^a		19.05±2.26 ^a	6.80±1.57	1.39±0.07 ^a		3.40±0.83 ^{a,b}	2.39±0.43 ^a	1.74±0.74		22.44±1.75 ^a	9.19±1.93	3.14±0.72	
<i>Abies-Quercus</i>	1.21±0.14	0.70±0.06 ^{a,b}	0.12±0.01 ^b		14.43±0.89 ^b	5.55±0.88	0.72±0.07 ^b		4.58±0.88 ^a	5.08±0.36 ^b	3.06±0.52		19.01±1.24 ^b	10.63±0.55	3.78±0.58	
<i>Abies-F.+Rh.</i>	1.07±0.13	0.54±0.04 ^b	0.08±0.01 ^c		15.25±0.37 ^b	5.02±1.24	0.53±0.09 ^b		3.44±0.28 ^{a,b}	5.02±0.60 ^b	3.43±1.59		18.70±0.64 ^b	10.04±1.71	3.79±1.72	
<i>Abies-Fargesia</i>	1.28±0.01	0.86±0.07 ^a	0.11±0.01 ^{a,b}		19.91±0.99 ^a	6.22±0.57	1.05±0.39 ^{a,b}		2.44±0.14 ^b	4.47±1.44 ^{a,b}	1.91±0.85		22.35±1.07 ^a	10.69±1.50	2.97±1.23	
$F_{3,11}$	3.98	15.23	32.48		16.25	1.41	10.31		5.90	7.02	2.04		10.92	0.64	0.41	
Difference (<i>p</i>)	n.s.	<0.01	<0.001		<0.001	n.s.	<0.01		<0.05	<0.05	n.s.		<0.01	n.s.	n.s.	

	Total nitrogen			Soluble sugars			Starch			non-structural carbohydrate		
	C- needles*	Fine roots	Sapwood	C- needles*	Fine roots	Sapwood	C- needles*	Fine roots	Sapwood	C- needles*	Fine roots	Sapwood
<i>C. lanceolata</i> (pure)	1.86±0.04	0.99±0.10 ^b	0.17±0.04 ^a	5.43±0.80 ^a	4.49±0.07 ^a	2.24±0.21	2.83±0.47	3.99±0.47 ^a	2.45±0.15	8.25±0.34 ^a	8.48±0.45 ^a	4.69±0.17
<i>C. lanceolata</i> +bamboos	1.92±0.05	1.42±0.14 ^a	0.09±0.03 ^b	2.31±0.33 ^b	3.26±0.31 ^b	1.53±0.22	2.63±0.26	2.41±0.16 ^b	2.76±0.92	4.94±0.54 ^b	5.66±0.24 ^b	4.29±1.13
<i>C. lanceolata</i> +shrubs	1.99±0.13	1.22±0.10 ^{a,b}	0.17±0.02 ^a	4.75±0.50 ^a	4.22±0.43 ^a	1.90±0.52	2.83±0.22	2.28±0.15 ^b	2.84±0.82	7.58±0.69 ^a	6.50±0.42 ^b	4.74±1.10
$F_{2\beta}$	1.555	10.315	5.961	24.392	13.364	3.157	0.367	30.245	0.244	31.400	43.455	0.220
Difference (p)	n.s.	< 0.05	< 0.05	< 0.001	< 0.01	n.s.	n.s.	< 0.001	n.s.	< 0.001	< 0.001	n.s.

higher temperature on the forest floor. Hence, effects of understorey shrubs on ecophysiology of overstorey trees were found to be more pronounced during the dry season than in the wet season (Fig. 2).

Management implications and suggestions for further research

Co-existing trees/herbs require water, CO₂, light, nitrogen, phosphorus, potassium and a common set of minor mineral nutrients. Different species acquire these resources in similar ways, and interspecific competition for these resources is the norm in plant communities (Barot 2004, Silvertown 2004). Plant-plant interaction can be classified as either competitive or facilitative, and divided mainly into aboveground and belowground categories (Montgomery et al. 2010). Negative and positive interactions of plants within a community have been intensely studied (Nambiar and Sands 1993, Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998, Montgomery et al. 2010), as mentioned in previous paragraphs. However, it is still poorly understood how the individual physiology responds to and reflects the balance between positive and negative interactions, and how those will change with rapid environmental changes (Fig. 3). For instance, Zhang et al. (2008, 2009a) experimentally revealed that plant-plant interactions such as intensity and importance of competition were altered by environmental changes.

For hundreds of years understorey removal and thinning have been used as effective forest management practices to improve the commercial timber worldwide. It is well-documented that thinning and understorey removal can not only reduce the competition but also improve the soil quality including soil temperature, water and nutrients availability, and further, enhance the growth rate (Roberts and Harrington

2008, Weiskittel et al. 2009, Zhang et al. 2009b, Tian et al. 2010). But, we still do not understand the physiological mechanism underlying those positive growth effects of thinning and understorey removal (Fig. 3). We also still do not know whether an enhanced growth rate of desired trees is caused by or correlated with increases in physiological activities (e.g., photosynthesis, water use efficiency, availability of nutrients and mobile carbohydrates, a balanced carbon gain and loss, etc.) of desired trees due to enhanced resource availability after management practice.

The present paper suggests that positive effects of thinning and understorey cut on target trees can be expected more rapidly and strongly in stressful area (e.g., low rainfall, nutrient-poor site) rather than in areas with optimal growth conditions, based on results shown in Figure 2. In that experiment (Fig. 2), the understorey biomass cut down was left on the forest floor to decompose *in situ*. The thinned biomass and the understorey biomass cut down in previous experiments, however, were normally removed from the forests studied. This means that the remained trees suffer directly from a net loss of nutrients contained in that biomass. Hence, it is needed to distinguish the effects of reduced nutrients storage from effects of reduced competition on remained trees. But anyway, through the present literature review we could conclude that the co-existing woody plants can affect the C- and N-physiology (Tables 1 and 2, Fig. 2), growth, and productivity in desired trees.

The present paper can help us to better understand the physiological mechanism for neighbor-dependent growth performance of trees, and to develop ecophysiology-based management strategies for dealing with neighboring plants in forest ecosystems. However, the world is facing the challenge of global warming and biodiversity loss. Hence, on the other hand, (1) the question of whether neighbor removal can also lead to fixing more CO₂ per unit area still awaits a conclusive answer; and (2) possible negative effects of neighbor removal on biodiversity conservation and soil erosion should also be taken into account.

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Figure 3. A diagram showing facilitative and competitive interactions and their effects on outcome at individual and community level. Negative and positive interactions and their effects on growth have been intensely studied, but it is poorly understood how net physiological responses of plants reflect the balance between mutualistic and competitive interactions, and how all those will be altered by a rapidly changing world.

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